

The contribution of root respiration of *Pinus koraiensis* seedlings to total soil respiration under elevated CO₂ concentrations

LIU Ying^{1,2}, HAN Shi-jie*, LI Xue-feng, ZHOU Yu-mei, ZHANG Jun-hui, JIA Xia

¹Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, P. R. China

²Graduate School of Chinese Academy of Sciences, Beijing 100039, P. R. China

Abstract: The impacts of elevated atmospheric CO₂ concentrations (500 $\mu\text{mol}\cdot\text{mol}^{-1}$ and 700 $\mu\text{mol}\cdot\text{mol}^{-1}$) on total soil respiration and the contribution of root respiration of *Pinus koraiensis* seedlings were investigated from May to October in 2003 at the Research Station of Changbai Mountain Forest Ecosystems, Chinese Academy of Sciences, Jilin Province, China. After four growing seasons in top-open chambers exposed to elevated CO₂, the total soil respiration and roots respiration of *Pinus koraiensis* seedlings were measured by a LI-6400-09 soil CO₂ flux chamber. Three PVC cylinders in each chamber were inserted about 30 cm into the soil instantaneously to terminate the supply of current photosynthates from the tree canopy to roots for separating the root respiration from total soil respiration. Soil respirations both inside and outside of the cylinders were measured on June 16, August 20 and October 8, respectively. The results indicated that: there was a marked diurnal change in air temperature and soil temperature at depth of 5 cm on June 16, the maximum of soil temperature at depth of 5 cm lagged behind that of air temperature, no differences in temperature between treatments were found ($P>0.05$). The total soil respiration and soil respiration with roots severed showed strong diurnal and seasonal patterns. There was marked difference in total soil respiration and soil respiration with roots severed between treatments ($P<0.01$); Mean total soil respiration and contribution of root under different treatments were 3.26, 4.78 and 1.47 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 11.5%, 43.1% and 27.9% on June 16, August 20 and October 8, respectively.

Keywords: Contribution of root respiration; Elevated CO₂; *Pinus koraiensis*; Root-severed technique; Soil respiration

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Introduction

Soils are the major reservoir of carbon in terrestrial ecosystems, containing more than two-thirds of total carbon in the terrestrial part of the biosphere. A major unknown in the response to anticipated climate changes is the extent to which forest ecosystems will become net sinks or sources of CO₂. The regulation of net primary production is well known for most of the earth's ecosystem, however, our knowledge about underground respiration processes under elevated atmospheric CO₂ is quite poor (Raich & Potter, 1995). Understanding soil carbon dynamics under elevated atmospheric CO₂ and temperature is thus critical for predicting future regional and global carbon budgets (Schimel 1995). Previous studies have suggested that the increasing atmospheric CO₂ concentration and temperature can stimulate soil CO₂ efflux (van Veen *et al.* 1991; Körner & Arnone 1992; Peterjohn *et al.* 1993, 1994; Johnson *et al.* 1994; Nakayama *et al.* 1994; Pajari 1995; Vose *et al.* 1995;

Hungate *et al.* 1997; Rey *et al.* 2001). However, there is relatively little information about which components of the soil CO₂ efflux are the most sensitive to the changes in atmospheric CO₂ (Paterson *et al.* 1997) or temperature.

Soil respiration includes three biological processes (soil microbes respiration, roots respiration and soil fauna respiration) and an abiotic process (oxidation of minerals containing carbon) (Singh & Gupta 1977). Roots are one of the major contributors to soil respiration. Field measurements are difficult because roots can not be extracted from the soil without any disturbance (Thierron and Laudelout 1996). Most of the direct measurements of roots respiration reported in the literature were performed with potted plants in a laboratory environment (Lambers *et al.* 1991). Hanson *et al.* (2000) reviewed and compared several methods for separating root and soil microbial contributions to soil respiration. Each approach has advantages and disadvantages. Limitations in available techniques to separate autotrophic (root) and soil heterotrophic respiration have hampered the understanding of forest carbon cycling. Autotrophic (root) respiration is here defined as respiration by roots, their associated mycorrhizal fungi and other microorganisms in the rhizosphere directly dependent on labile C compounds leaked from roots.

In this study, subtraction method (Gansert 1994; Högberg *et al.* 2001) is adopted and LI-6400-09 soil respiration chamber (LI-COR Inc., Lincoln, Nebraska, USA) is used to

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Biography: LIU Ying (1976-), female, Ph. D., Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, P. R. China.

E-mail: liuyingamy@163.com

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***Corresponding author.** Tel: 024-83970443. Email: hansj@163.com

measure soil respiration rates with and without roots severed *in situ* in Korean pine (*Pinus koraiensis*) seedlings after four growing seasons exposure to elevated CO₂ in top-open chambers. Therefore, the contribution of roots to total soil respiration is evaluated. This approach overcomes potential concerns about the disturbance of soils, which would otherwise be a significant limitation for the study of natural responses by ecosystems.

Materials and methods

Site description

The study site is situated at the Research Station of Changbai Mountain Forest Ecosystems, Chinese Academy of Sciences (42°24'N, 128°28'E; 738 m in elevation) in the northeast China. The climate of this area is characterized by temperate zone continental climate, with cold and lengthy winters and warm and rainy summers. The mean annual precipitation is about 700 mm, mean annual temperature is about 3.5°C, and the frost-free period is about 100-120 d.

Elevated CO₂ treatments

In 1999, Korean pine was planted in the top-open chambers (OTCs) and in the open field. The soil is dark brown forest soil. Seedlings were treated by high CO₂ concentrations continuously (24 h·d⁻¹) during growing season from 1999 to 2003. All plants were irrigated to maintain approximately similar soil moisture. Top-open chamber consists of aluminum frames of 1.2 m in length, 0.9 m in width and height and clear glass covers. The seedlings of Korean pine were treated with three levels of CO₂: 700 μmol·mol⁻¹ CO₂, 500 μmol·mol⁻¹ CO₂, control chamber, and open field (ambient CO₂, approximately 350 μmol·mol⁻¹). Atmospheric CO₂ concentration in each terracoscum was monitored continuously using a LCA4 photosynthesis analyzer (ADC, UK) that was calibrated regularly with CO₂ standards. All measurements were made on five-year-old seedlings after they had been exposed to specific treatment for four growing seasons from their emergence. The height of the seedlings is about 30 cm and the density is 60 seedlings per square meter.

Measurement of soil respiration and root respiration

Steel cylinder tubes with 10.5-cm inner-diameter were inserted into the soil about 30 cm in depth (there were almost no roots below this depth) to sever fine roots in each top-open chamber. The steel cylinder was then replaced with PVC (polyvinyl chloride) cylinders with inner diameters and lengths equal to that of the steel cylinder. After one month, soil respirations both inside (soil respiration with roots severed) and outside the cylinders were measured every 3 h during daytime and every 4 h at night from June 15 to 16, 2003 using a LI-6400-09 soil respiration chamber. After four months, soil respiration was measured again on October 8, 2003. The soil chamber is coupled to a LI-6400

photosynthesis system that computes the emissions from the soil to the chamber. Soil temperature at a depth of 5 cm and air temperature were measured concurrently with a temperature probe attached to the photosynthesis analyzer.

Results

Diurnal changes of air and soil temperatures at depth of 5 cm, total and root severed soil respirations

During the soil respiration measurements the diurnal air temperature and soil temperature at depth of 5 cm ranged from 12.88°C to 30.29°C and from 11.19°C to 25.91°C, respectively (Figs.1, 2, 3 and 4). The temperatures increased in the morning and decreased in the afternoon. In general, air temperature was higher than soil temperature at depth of 5 cm. However, they tended to be the same before sunrise. The maximum soil temperature at depth of 5 cm lagged behind that of air temperature. No differences in air temperature and soil temperature were found at depth of 5 cm between treatments.

Both total soil respiration and soil respiration with roots severed showed a strong diurnal pattern, increasing from before sunrise to about 14:00 in the afternoon and then decreased until the next day before sunrise (Figs. 1, 2, 3 and 4). The pattern of soil respiration was similar to that of temperature, which indicated that soil respiration rates were affected by temperature greatly.

The regressions of soil respiration rate and soil temperature at depth of 5 cm indicated that there were significantly logarithmic correlations between them (Table.1).

Table 1. Correlation equations between soil respiration (Rs) rate and soil temperature (Ts) at depth of 5 cm

| Soil respiration | Site | Equation | r |
|-------------------------------------|------|-----------------------|------|
| Total soil respiration | A | $Rs=2.04\ln(Ts)-1.72$ | 0.78 |
| | B | $Rs=3.81\ln(Ts)-7.32$ | 0.82 |
| | C | $Rs=1.70\ln(Ts)-2.10$ | 0.87 |
| | D | $Rs=1.78\ln(Ts)-1.89$ | 0.69 |
| Soil respiration with roots severed | A | $Rs=1.66\ln(Ts)-1.51$ | 0.78 |
| | B | $Rs=3.02\ln(Ts)-5.45$ | 0.87 |
| | C | $Rs=1.82\ln(Ts)-2.66$ | 0.91 |
| | D | $Rs=1.89\ln(Ts)-2.51$ | 0.69 |

Note: A: the open field; B: control chamber; C: 500 μmol·mol⁻¹ CO₂ chamber; D: 700 μmol·mol⁻¹ CO₂ chamber.

Effects of elevated CO₂ on total soil respiration rate and contribution of root respiration to the total soil respiration and seasonal variations of them

The values of total soil respiration in the open field, control chamber and elevated CO₂ (500 μmol·mol⁻¹ CO₂, 700 μmol·mol⁻¹ CO₂) chambers were 3.96, 3.24, 2.63, 3.19 μmol·m⁻²·s⁻¹, respectively, which is the highest in open field and the lowest in 500 μmol·mol⁻¹ CO₂ chamber on June 16. However, soil respiration rate in the open field was

lower than that in other chambers on August 20. There was an increase of soil respiration rate with the increase of CO₂

concentration on October 8 (Fig. 5).

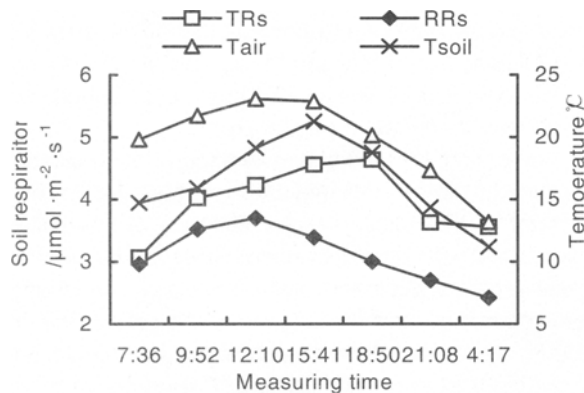


Fig.1 Diurnal variations of total and soil respiration with roots severed, air and soil temperatures at depth of 5 cm in the open field

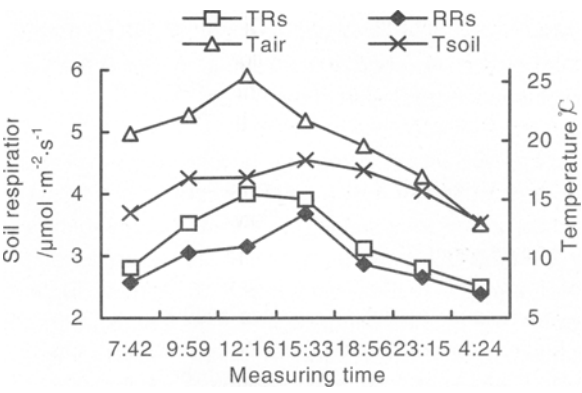


Fig.2 Diurnal variations of total and soil respiration with root severed, air and soil temperatures at depth of 5 cm in control chamber

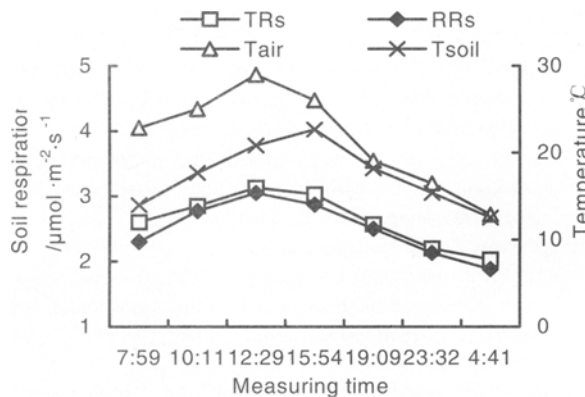


Fig.3 Diurnal variations of total and soil respiration with roots severed, air and soil temperatures at depth of 5 cm in 500 μmol·mol⁻¹ CO₂ chamber

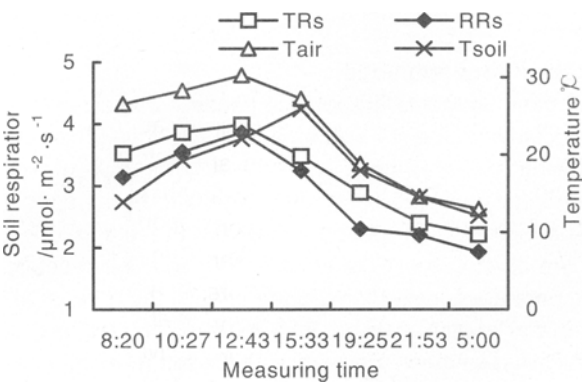


Fig.4 Diurnal variations of total and soil respiration with roots severed, air and soil temperature at depth of 5 cm in 700 μmol·mol⁻¹ CO₂ chamber

TRs: Total soil respiration rate; RRs: soil respiration rate with roots severed; Tair: air temperature; Tsoil: soil temperature

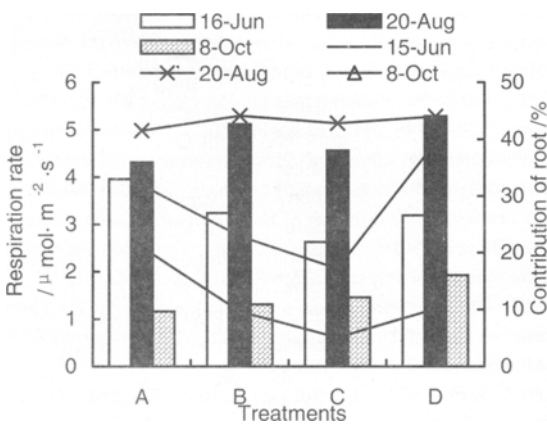


Fig.5 Total soil respiration and contribution under different treatments in different months

Based on the analysis of Fig. 5, it was found that soil respiration rates in different treatments were the highest on August 20 and the lowest on October 8. The contribution of root respiration to the total soil respiration had a similar pattern to soil respiration with the changes of seasons.

Discussion

Effects of elevated CO₂ and contribution of root respiration to the total soil respiration

Elevated CO₂ can increase (Rouhier *et al.* 1996; Janssens *et al.* 1998; Lin *et al.* 1999), decrease (Gifford *et al.* 1985; Callaway *et al.* 1994) or have no effect (Oberbauer *et al.* 1986; den Hertog *et al.* 1993) on soil respiration and contribution of roots. Therefore, it is difficult to draw any definitive conclusions on the effects of elevated CO₂ on respiratory processes. The discrepancy and lack of uni-

formity in specific soil respiration responses to elevated CO₂ could be attributed to a number of factors, including the methods utilized, the concentration of CO₂ at which the measurements were made (Qi *et al.* 1994; Burton *et al.* 1997), the tree species investigated (Lee & Jarvis, 1995), growth conditions, duration of the treatment, age of the tree seedlings, and interpretation of the results.

There was significant difference in total soil respiration and the contribution of root between treatments ($P < 0.01$). No increase in the total soil respiration and contribution of root by elevated CO₂ treatments was observed on June 16. However, opposite results were found on August 20 and October 8. The reasons might be that: The first experiment was conducted about two weeks after the seedlings were exposed to elevated CO₂ concentrations, when elevated CO₂ had not affected them. After the treatments of several months, both soil CO₂ concentration and carbon allocation of seedlings to roots might be increased, which may have caused the increase of soil respiration on August 20 and October 8.

Estimate of root respiration

Field measurements are difficult because roots can not be extracted from the soil without any disturbance (Thierron & Laudelout, 1996; Hanson *et al.* 2000). Most of the direct measurements of root respiration reported in literatures were performed with potted plants in the laboratories (Lambers *et al.* 1991). Furthermore, they may have different temperature sensitivities (Boone *et al.* 1998; Atkin *et al.* 2000; Epron *et al.* 2001) and their relative contributions to the total soil respiration may vary with season (Hanson *et al.* 2000; Epron *et al.* 2001). Estimates of the contribution of root respiration to total soil respiration vary as widely as between 10% and 90% depending upon the type of ecosystem studied and the method used (Hanson *et al.* 2000). Although many attempts have been made to estimate the root contribution to total soil respiration, it is difficult to compare results estimated by different methods because each method has its own limitations (Behara *et al.* 1990). Therefore, our results were compared with the results obtained from similar methods, such as the clear-cutting or girdling method.

In this study, we found that the mean contribution of root to total soil respiration in different treatments were 11.5%, 43.1%, and 27.9% on June 16, August 20, and October 8, respectively (Fig. 5). This was somewhat lower than that calculated in the previous studies (Nakane *et al.* 1996; Ohashi *et al.* 2000; Högborg *et al.* 2001; Bhupinderpal-singh *et al.* 2003). However, the estimate of the contribution of roots respiration to total soil respiration may be conservative. The first experiment was conducted after the roots had been severed about one month, when root carbohydrate reserves were probably mobilized to support root function in the absence of a supply from aboveground. In addition, increased root death may have stimulated

greater respiration levels of heterotrophic (decomposer) organisms than those that would naturally occur in forests. Lee *et al.* (2003) found that root respiration is negligible by 3 months after root excision. Therefore, the contribution of root on August 20 was higher than that on June 16. The last experiment was conducted in the end of growing season, when roots activity was small. Thus, the contribution of root was lower than that on August 20.

Comparing the total soil respiration rates *in situ* and soil respiration with roots severed enables us to estimate natural root respiration in the absence of any soil disturbance and with little labor force. However, this method necessitates consideration of the effects of any changes in environmental conditions after severing root. In the present study, the same environmental conditions could be controlled in the top-open chambers. Therefore, we concluded that this approach is one simple and effective method for estimating the contribution of root respiration to total soil respiration.

References

- Atkin, O.K., Edwards, E.J. and Loveys, B.R. 2000. Response of root respiration to changes in temperature and its relevance to global warming [J]. *New Phytologist*, **147**: 141-154.
- Behara, N., Joshi, S.K., Pati, D.P. 1990. Root contribution to total soil metabolism in a tropical forest soil from Orissa, India [J]. *Forest Ecology and Management*, **36**: 125-134.
- Bhupinderpal-singh, Nordgren, A. Ottosson Lofvenius, M. Högborg, M.N., Emellander, P.E and Högborg, P. 2003. Tree root and soil respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year [J]. *Plant, Cell and Environment*, **26**: 1287-1296.
- Boone, R.D., Nadelhoffer, K.J., Canary, J.D. *et al.* 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration [J]. *Nature*, **396**: 570-572.
- Brumme, R. 1995. Mechanisms of carbon and nutrient release and retention in beech forest gaps [J]. *Plant and Soil*, **168/169**: 593-600.
- Burton, A.J., Zogg, G.P., Pregitzer, K.S., Zak, D.R. 1997. Effect of measurement CO₂ concentration on sugar maple root respiration [J]. *Tree Physiology*, **17**: 421-427.
- Callaway, R.M., DeLucia, E.H., Thomas, E.M., Schlesinger, W.H. 1994. Compensatory responses of CO₂ exchange and biomass allocation and their effects on the relative growth-rate of ponderosa pine in different CO₂ and temperature regimes [J]. *Oecologia*, **98**: 159-166.
- den Hertog, J., Stulen, I. and Lambers, H. 1993. Assimilation, respiration and allocation of carbon in *Plantago major* as affected by atmospheric CO₂ levels - a case-study [J]. *Vegetatio*, **104**: 369-378.
- Epron, D., le Dantec, V., Dufrene, E. and Granier, A. 2001. Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest [J]. *Tree Physiology*, **21**: 145-152.
- Gansert, D. 1994. Root respiration and its importance for the carbon balance of beech saplings (*Fagus sylvatica* L.) in a montane beech forest [J]. *Plant and Soil*, **167**: 109-119.
- Gifford, R.M., Lambers, H., Morison, J.I.L. 1985. Respiration of crop species under CO₂ enrichment [J]. *Physiologia Plantarum*, **63**: 351-356.
- Hanson, P.J., Edwards, N.T., Garten, C.T. and Andrews, J.A. 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations [J]. *Biogeochemistry*, **48**:

- 115-146.
- Högborg, P., Nordgren, A., Buchmann, N., *et al.* 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration [J]. *Nature*, **411**: 789-792.
- Hungate, B.A., Holland, E.A., Jackson, R.B., Chapin iii, Mooney, H.A., Field, C.B. 1997. The fate of carbon in grasslands under carbon dioxide enrichment [J]. *Nature*, **388**: 576-579.
- Janssens, I.A., Crookshanks, M., Taylor, G. and Ceulemans, R. 1998. Elevated atmospheric CO₂ increase fine production, respiration, rhizosphere respiration and soil CO₂ efflux in Scots pine seedlings [J]. *Global Change Biology*, **4**(8): 871-883.
- Johnson, D., Geisinger, D., Walker, R., Newman, J., Vose, J., Elliot, K. and Ball, T. 1994. Soil pCO₂, soil respiration, and root activity CO₂-gumigated and nitrogen-fertilized ponderosa pine [J]. *Plant and Soil*, **165**: 129-138.
- Körner, C. and Arnone, J.A. 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems [J]. *Science*, **257**: 1672-1675.
- Lambers, H., van der Werf, A. and Konings, H. 1991. Respiratory patterns in roots in relation to their functioning. In: Waisel Y, Eshel A, Kafkafi U, eds. *Plant root: the hidden half* [C]. New York, USA: Marcel Dekker, p229-263.
- Lee, H.S.J. and Jarvis, P.G. 1995. Trees differ from crops and from each other in their responses to increases in CO₂ concentration [J]. *Journal of Biogeography*, **22**: 323-330.
- Lee, M., Nakane, K., Nakatsubo, T. and Koizumi, H. 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest [J]. *Plant and Soil*, **255**: 311-318.
- Lin, G., James, Ehleringer, R. Paul, Rygielwicz, T. Mark, G. *et al.* 1999. Elevated CO₂ and temperature impacts on different components of soil CO₂ efflux in Douglas-fir terraces [J]. *Global Change Biology*, **5**(2): 157-166.
- Nakane, K., Kohno, T., Horikoshi, T. 1996. Root respiration rate before and just after clear-felling in a mature, deciduous, broad-leaved forest [J]. *Ecological Research*, **11**: 111-119.
- Nakayama, F.S., Huluka, G., Kimball, B.A., Lewin, K.F., Nagy, J., Hendrey, G.R. 1994. Soil carbon dioxide fluxes in natural and CO₂-enriched systems [J]. *Agricultural and Forest Meteorology*, **70**: 131-140.
- Oberbauer, S.F., Oechel, W.C., Riechers, G.H. 1986. Soil respiration of Alaskan tundra at elevated atmospheric carbon dioxide concentrations [J]. *Plant and Soil*, **96**: 145-148.
- Ohashi, M., Gyokusen, K. and Saito, A. 2000. Contribution of root respiration to total soil respiration in a Japanese cedar (*Cryptomeria japonica* D. Don) artificial forest [J]. *Ecological Research*, **15**(3): 323-333.
- Pajari, B. 1995. Soil respiration in a poor upland site of scots pine stand subjected to elevated temperatures and atmospheric carbon concentration [J]. *Plant and Soil*, **169**: 563-570.
- Paterson, E., Hall, J.M., Rattray, E.A.S., Griffiths, B.S., Ritz, K., Killham, K. 1997. Effects of elevated CO₂ on rhizosphere carbon flow and soil microbial processes [J]. *Global Change Biology*, **3**: 363-377.
- Peterjohn, W.T., Melillo, J.M., Bowles, F.P., Steudler, P.A. 1993. Soil warming and trace gas fluxes - experimental design and preliminary flux results [J]. *Oecologia*, **93**: 18-24.
- Peterjohn, W.T., Melillo, J.M., Steudler, P.A. *et al.* 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures [J]. *Ecological Applications*, **4**: 617-625.
- Qi, J., Marshall, J.D., Mattson, K.G. 1994. High soil carbon dioxide concentrations inhibit root respiration of Douglas fir [J]. *New Phytologist*, **128**: 435-442.
- Raich, J.W. and Potter, C.S. 1995. Global patterns of carbon dioxide emissions from soils [J]. *Global Biogeochemical Cycles*, **9**: 23-36.
- Rey, A., Pegoraro, E., Tedeschi, V., Tedeschi, V., Parri, I.D., Jarvis, P.G. and Valentini, R. 2001. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy [J]. *Global change Biology*, **8**: 851-866.
- Rouhier, H., Billès, G., Billès, L., Bottner, P. 1996. Carbon fluxes in the rhizosphere of sweet chestnut seedlings (*Castanea sativa*) grown under two atmospheric CO₂ concentrations - C¹⁴ partitioning after pulse labelling [J]. *Plant and Soil*, **180**: 101-111.
- Schimel, D.S. 1995. Terrestrial ecosystems and carbon cycle [J]. *Global Change Biology*, **1**: 77-91.
- Singh, J.S. and Gupta, S.R. 1977. Plant decomposition and soil respiration in terrestrial ecosystems [J]. *Botanical Review*, **43**: 449-528.
- Thierron, V. and Laudelout, H. 1996. Contribution of root respiration to total CO₂ efflux from the soil of a deciduous forest [J]. *Canadian Journal of Forest Research*, **26**(7): 1142-1148.
- van Veen, J.A., Liljeroth, E., Lekkerkerk, L.J.A., van de Geijn, S.C. 1991. Carbon fluxes in plant-soil systems at elevated atmospheric CO₂ levels [J]. *Ecological Applications*, **1**: 175-181.
- Vose, J.M., Elliott, K.J., Johnson, D.W., Walker, R.F. *et al.* 1995. Effects of elevated CO₂ and N fertilization on soil respiration from ponderosa pine (*Pinus ponderosa*) in open-top chambers [J]. *Canadian Journal of Forest Research*, **25**: 1243-1251.